A new species of *Felimare* (formerly *Mexichromis*) (Gastropoda: Opisthobranchia: Chromodorididae) from the Yucatan Peninsula, Mexico

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ABSTRACT

A new species of chromodorid nudibranch from the western Atlantic is described based on three specimens collected in the Campeche Bank, Gulf of Mexico. This new species is assigned to *Felimare*, an allocation based on a new classification of the Chromodorididae established with molecular data. The anatomy and molecular data for this new species are compared to those of other Atlantic species previously assigned to *Mexichromis* (now part of *Felimare*). The new species is characterized by having a primarily white dorsum with two longitudinal blue lines, as well as a yellow band surrounding the mantle margin. Mitochondrial 16S gene data confirms that the new species is genetically different from other Atlantic species of *Felimare* for which molecular data is available.

Additional keywords: Nudibranchia, Gulf of Mexico, 16S mtDNA, anatomy

INTRODUCTION

Rudman (1984) defined *Mexichromis* Bertsch, 1977 (type species *Chromodoris antonii* Bertsch, 1976), as well as other genera of Chromodorididae, based on several anatomical characteristics, primarily the morphology of the mantle glands, oral tube, jaw rodlets, radular teeth, and reproductive system. According to Rudman (1984), *Mexichromis* includes species with mantle glands open ventrally and restricted to a few large glands posteriorly and a few smaller ones along each side; oral tube at least four times the length of the buccal bulb and at least twice the diameter; jaw rodlets ranging from bicuspid to multicuspid; radular teeth bicuspid and denticulate, the denticles being as large or nearly as large as the cusps; reproductive system with a large ramifying vestibular gland covering the ventral surface of the female gland mass and a large exogenous sperm sac (bursa copulatrix) lying down the wide muscular vagina. Although *Mexichromis* initially included only eastern Pacific species (Bertsch, 1977), Rudman (1983, 1984) transferred the tropical Indo-Pacific species *M. mariei* (Crosse, 1872), *M. festiva* (Angas, 1864), *M. macropa* Rudman, 1983, and *M. multituberculata* (Baba, 1953) to this genus. Since then, four additional species have been added to this group (Ortea et al., 1996), including the western Atlantic species *M. kempfi* (Ev. Marcus, 1971) and *M. molloi* Ortea and Valdés, 1996, and the eastern Atlantic species *M. francoisae* (Bouchet, 1980) and *M. garciagomezi* Ortea and Valdés, 1996.

Recently, Johnson and Gosliner (2012), based on molecular data, reorganized the classification of the Chromodorididae and found that the traditional group *Mexichromis* is paraphyletic. According to this new scheme, the eastern Pacific and Caribbean species *M. porterae* (Cockerell, 1901) and *M. kempfi* are transferred to *Felimare* Marcus and Marcus, 1967 along with other eastern Pacific and Atlantic species previously assigned to *Hypselodoris* Stimpson, 1855, whereas *Mexichromis* is maintained for *M. antonii*, the type species, as well as species previously assigned to *Durvilledoris* Rudman, 1984 and *Pectenodoris* Rudman, 1984, and all the tropical Indo-Pacific species of *Mexichromis*.

Although not explicitly tested in their phylogenetic analysis, Johnson and Gosliner (2012) hypothesized that most Atlantic species traditionally assigned to *Mexichromis* likely belong to *Felimare*, including *M. francoisae*, *M. molloi*, whereas eastern Pacific species belong to *Mexichromis*, including *M. tica* Gosliner, Ortea and Valdés, 2004 and *M. tura* (Marcus and Marcus, 1967).

In this paper, a new species of Atlantic chromodorid nudibranch is described based on specimens collected in the Yucatan Peninsula, Mexico. The external morphology and anatomy of this new species is consistent with those of the group traditionally defined as *Mexichromis*, but now considered *Felimare* (Johnson and Gosliner 2012).

MATERIALS AND METHODS

Collection and Preservation: The Campeche Bank is composed of small reefs and cays located in the northwestern sector of the Yucatan Peninsula. The bank reaches 60 m depth (Spalding, 2004). The specimens here studied were collected by hand in the Madagascar Reef, within the Campeche Bank (Ortigosa-Gutiérrez, 2009) as part of a multidisciplinary project aiming to describe the diversity of the main groups of invertebrates (corals, echinoderms, crabs, and shrimps) that inhabit some reefs of the Campeche Bank. The Madagascar Reef is located 40 km offshore and ranges in depth from 4 to 14 m (Zarco-Perelló, 2008). All the specimens were photographed alive, then relaxed with clove oil, and fixed and preserved in absolute ethanol. The type material is deposited in the collections of the Colección Nacional de Malacología, Instituto de Biología, Universidad Nacional Autónoma de México (CNMO) and the Natural History Museum of Los Angeles County (LACM).

Morphological Examination: The specimens were dissected and the reproductive system examined and drawn using a dissecting microscope with camera lucida. The buccal mass of one individual was removed and dissolved in 10% sodium hydroxide, and the radula and jaw examined using a scanning electron microscope (SEM) Hitachi S-3000N at the LACM.

DNA Extraction: DNA extraction was performed using either a hot Chelex® protocol or the DNeasy® Blood and Tissue Kit (Qiagen). Approximately 1–3 mg of the foot was cut into fine pieces for extraction for both protocols. For the Chelex® extraction, the foot tissue was rinsed and rehydrated using 1.0 mL TE buffer (10 mM Tris, 1 mM EDTA, pH 8.0) for 20 minutes. A 10% (w/v) Chelex® 100 (100–200 mesh, sodium form, Bio-Rad) solution was prepared using TE buffer. After rehydration, the tissue mixture was then centrifuged, 975.00 µL of the supernatant was removed, and 175.00 µL of the Chelex® solution was added. Samples were then heated in a 56°C water bath for 20 minutes, heated in a 100°C heating block for 8 minutes, and the supernatant was used for PCR. The DNeasy protocol supplied by the manufacturer was followed, with some modifications. The elution step was modified such that the first elution was collected using 100.00 µL of Buffer AE and was allowed to incubate at room temperature for 5 minutes before centrifugation. In a new test tube, a second elution step was conducted using 200.00 µL of Buffer AE and was also allowed to incubate at room temperature for 5 minutes before centrifugation. The first elution was used for PCR.

PCR Amplification and Sequencing: Palumbi's universal 16S primers (Palumbi, 1996), as well as internal primers for 16S designed for another group of opisthobranchs (Ornelas-Gatdula et al., 2011) were used to amplify the regions of interest. Multiple attempts to obtain CO1 or complete 16S sequences using different primers were unsuccessful.

The master mix was prepared using 34.75 µL H_2O, 5.00 µL Buffer B (ExACTGene, Fisher Scientific), 5.00 µL 25 mM $MgCl_2$, 1.00 µL 40mM dNTPs, 1.00 µL 10mM primer 1, 1.00 µL primer 2, 0.25 µL 5 mg/mL Taq, and 2.00 µL extracted DNA. Reaction conditions were as follows: an initial denaturation for 2 min at 94°C, 35 cycles of (1) denaturation for 30 sec at 94°C, (2) annealing for 30 sec at 50°C, and (3) elongation for 1 min at 72°C, and a final elongation for 7 min at 72°C. PCR product yielding a band of appropriate size, each approximately 250 bp in length, for 16S (16Sar-L + 16Sbr-FAP) was purified using the Montage PCR Cleanup Kit (Millipore). Cleaned PCR samples were quantified using a NanoDrop 1000 Spectrophotometer (Thermo Scientific). Each primer was diluted to 2.0 pmol/µL for sequencing with the PCR products. PCR products were diluted to 6.0 ng/µL. Samples were sequenced at the City of Hope DNA Sequencing Laboratory (Duarte, CA) using chemistry types BigDye V1.1.

Phylogenetic Analyses: Sequences were assembled and edited using Geneious Pro 4.7.4 (Biomatters Ltd.). Geneious was also used to extract the consensus sequence between the primer regions and to construct the alignment for each gene using the default parameters. A total of 250 bp were amplified from the new species and used for the phylogenetic analyses (GenBank accession number JX101321). For comparison purposes, several GenBank sequences belonging to *Mexichromis* (as defined by Johnson and Gosliner, 2012) were downloaded from GenBank: *Mexichromis antonii* (EU982800), *Mexichromis maeropa* (EF534050), *Mexichromis mariei* (EF534049), *Mexichromis festiva* (EF534051), *Mexichromis aurora* (EU982805), *Mexichromis trilineata* (EU982806), *Mexichromis lemniseata* (EU982790), and *Mexichromis similaris* (EF534055), and so were sequences belonging to *Felimare* (as defined by Johnson and Gosliner, 2012): *Felimare orsinii* (AJ225189), *Felimare villafranca* (AF249237), *Felimare bilineata* (EF534052), *Felimare californiensis* (EU982796), *Felimare picta* (AF249238), *Felimare picta verdensis* (HM162594), *Felimare ruthae* (EU982799), *Felimare kempfi* (EF534047), *Felimare porterae* (EF534067). *Hypselodoris infuscata* (FJ917426) was selected as the outgroup.

The Akaike Information Criterion (Akaike 1974) was executed in MrModeltest v2.3 (Nylander 2004), to determine the best-fit model of evolution. MrModeltest selected GTR+I+G as the best-fit evolutionary model for the data set and estimated the following parameters: Base frequencies (A = 0.3623, C = 0.1202, G = 0.1679, T = 0.3496); Rate matrix ([A-C] = 0.9228, [A-G] = 9.0170, [A-T] = 3.1131, [C-G] = 0.1367, [C-T] = 9.2412); Proportion of invariable sites = 0.3260; Gamma distribution shape parameter = 0.5376. The resulting MrBayes block model line was: lset nst=6 rates=invgamma.

A Bayesian analysis was executed in MrBayes v3.1.2 (Huelsenbeck and Ronquist 2001). The Markov chain

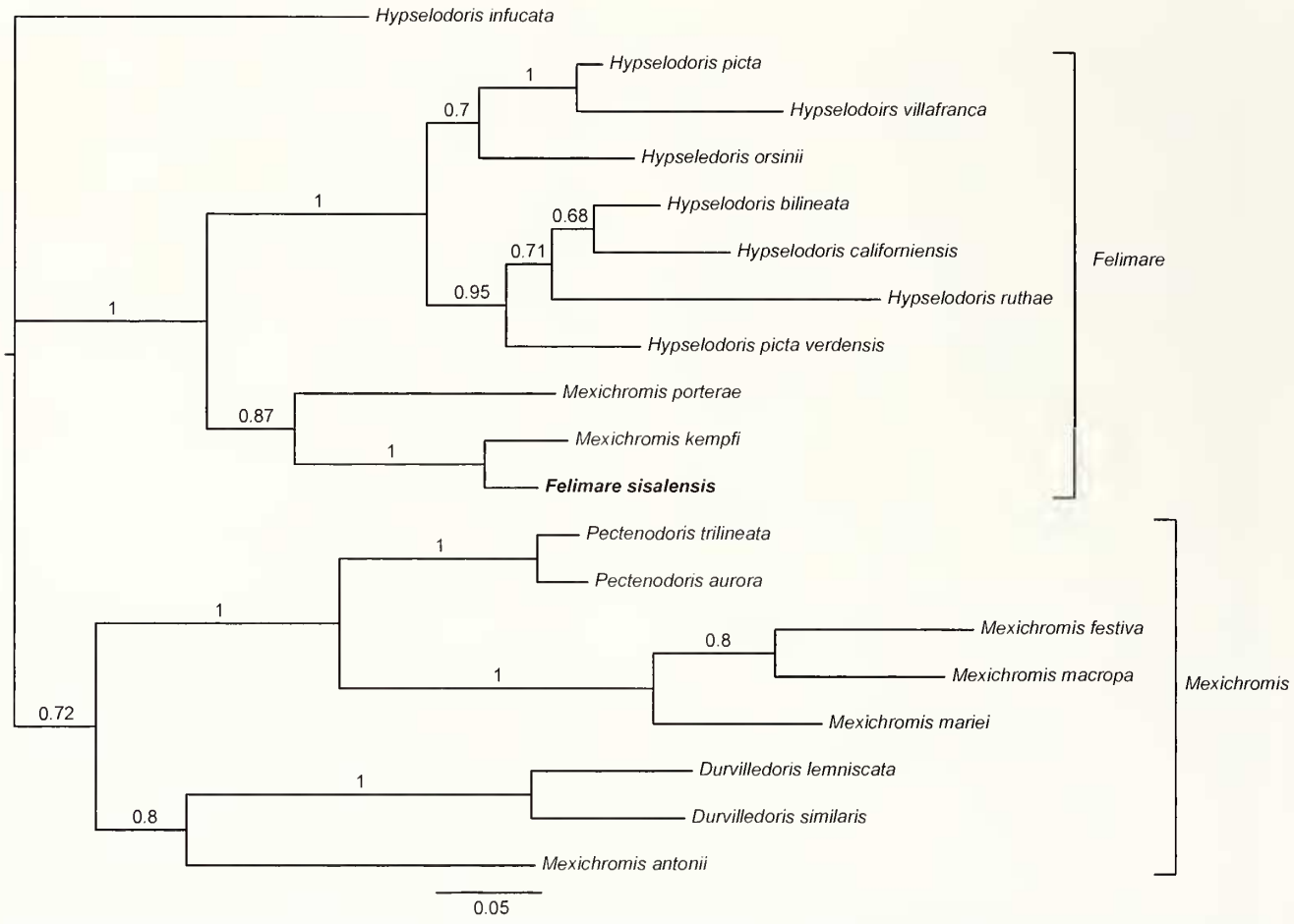

Figure 1. Bayesian tree of 16S sequences. Posterior probabilities are shown only for nodes with values over 0.5. Binominal combinations are the same as used in GenBank, reflecting the established nomenclature before Johnson and Gosliner (2012).

Monte Carlo analysis was run with two runs of six chains for ten million generations, with sampling every 100 generations. All other settings remained in the default. The default 25% burn-in was applied before constructing majority-rule consensus tree. The remaining 150,000 trees were used to construct majority rule consensus trees and calculate posterior probabilities. All clades and support values are shown in the resulting phylogenies. All posterior probabilities are mapped on all trees.

RESULTS

Molecular Data (Figure 1): The Bayesian consensus phylogram (Figure 1) is consistent with the results obtained by Johnson and Gosliner (2012) despite the fact that only one gene was analyzed, although it lacks support in several areas. This phylogeny confirms that *Felimare* is monophyletic (posterior probability = 1.0) and includes Atlantic species previously included in *Hypselodoris* and *Mexichromis* as well as *F. porterae*. Within *Felimare*, species with bicuspid radular teeth (previously classified as *Hypselodoris*) are also monophyletic (posterior probability = 1.0), whereas eastern Pacific and Atlantic species previously classified as *Mexichromis* are clustered in a poorly supported clade. The new species described herein is in this group, confirming the morphological hypothesis of classification proposed in this study.

The rest of the species included in the analysis (formerly *Pectenodoris*, *Durvilledoris* and Indo-Pacific and one eastern Pacific *Mexichromis*) are not supported as monophyletic, but both sample size and gene coverage are too limited to reach any conclusion about the classification of larger groups of the Chromodorididae.

This analysis confirms the position of the new species here described in *Felimare*. It also shows that this species appears to be sister to *F. kempfi* (posterior probability = 1.0), but these two species are genetically distinct in the 16S gene. In the short fragment obtained (250 bp) there were 96.6% of identical sites between the new species and *F. kempfi* which is equivalent to level of sequence similarity between other sister species of Chromodorididae; in the same fragment there were 97.0% of identical sites between *M. aurora* and *M. trilineata*.

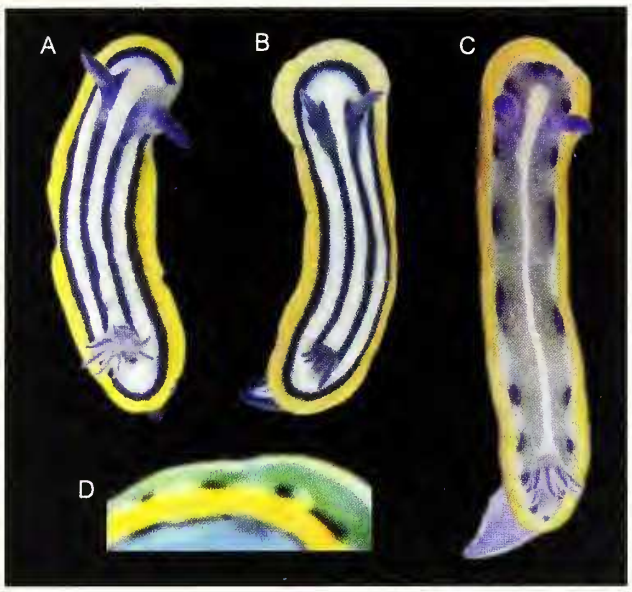

Figure 2. Photographs of live animals. A. Dorsal view of a paratype of *Felimare sisalensis* sp. nov., 11 mm long (LACM 3223), B. Dorsal view of the holotype of *Felimare sisalensis*, 12 mm long (CNMO 3037). C. Dorsal view of a juvenile specimen of *Felimare kempfi* from Campeche Bank, 14 mm long. D. Lateral view of the mantle margin of a juvenile specimen of *F. kempfi* (7 mm long) showing the characteristic black spots.

Morphological Data (Figures 2A–B, 3, 4): The examination of the morphological data conformed that the material here examined represents a new species. The following sections contain the formal description.

SYSTEMATICS

Chromodorididae Bergh, 1981

Felimare

***Felimare sisalensis* new species (Figures 2A–B, 3, 4)**

External Morphology (Figures 2A-B): The body is opaque white with two blue lines that run from each rhinophore to the gill, surrounding it. The mantle edge is surrounded by a yellow band, followed by a thinner blue band. The branchial leaves and rhinophores are blue and retract into pockets. There are nine unnipinnate branchial leaves. The foot sole is opaque white and is surrounded by a blue line. The mantle margin contains one band of small, rounded mantle glands, except for the anterior end of the body.

Reproductive system (Figure 3): The deferent duct is wide and short, followed by a long and narrow prostate. The vagina is short and narrow. The uterine duct connects into the vagina. The bursa copulatrix is large and oval in shape. The seminal receptacle is somewhat elongated and connects into the vagina, at the base of

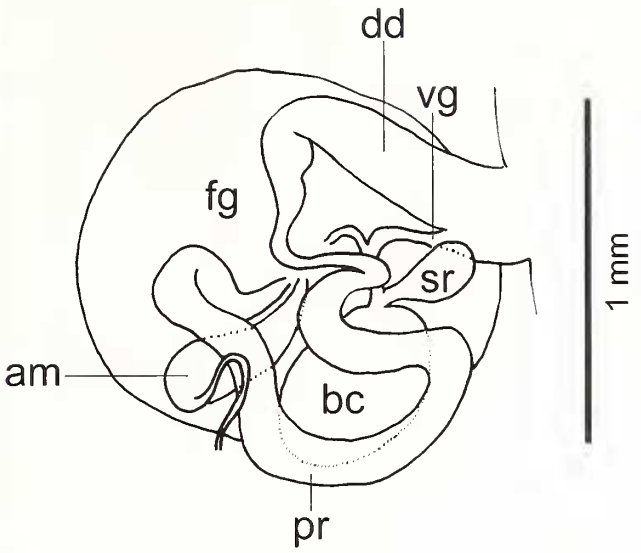

Figure 3. Reproductive system of a paratype of *F. sisalensis* (CNMO 2981). Abbreviations: **am:** ampulla; **bc:** bursa copulatrix; **dd:** deferent duct; **fg:** female gland complex; **pr:** prostate; **sr:** seminal receptacle; **ud:** uterine duct; **va:** vagina; **vg:** vestibular gland.

the bursa copulatrix. The ampulla is relatively short, and straight, with no visible folds. The female gland complex is large, almost the same size that the rest of the reproductive systems. A vestibular gland was not observed, but due to the small size of the reproductive systems it possible that it was overlooked.

Radula and Jaw (Figure 4): The radular formula is 38 × 20.0.20 in a paratype (CNMO2981). There are no rachidian teeth. All lateral teeth are similar in shape and size, with no clear distinction between inner, mid and outer lateral teeth. All teeth are hook-shaped, elongate, with 4-6 denticles. The jaw consists of numerous short, tricuspid rodlets.

Type Material: HOLOTYPE: 12 mm long (CNMO 3037). PARATYPES. 1 specimen 11 mm long (LACM 3223) and 1 specimen 12 mm long (CNMO 2981).

Type Locality: Madagascar Reef, Campeche Bank, Yucatan, Mexico (21°26′28.3″ N, 90°17′22.8″ W), 4 September 2007, 7 m depth. All specimens were collected on green algae.

Geographic Distribution: This species has only been collected on Madagascar Reef, Campeche Bank, Yucatan, Mexico.

Etymology: The species is named in honor of the village of Sisal, Yucatan, Mexico, were the Umdi-Sisal, UNAM station is located.

DISCUSSION

Among the Atlantic species of *Felimare*, only four (those previously assigned to *Mexichromis*) have radular teeth

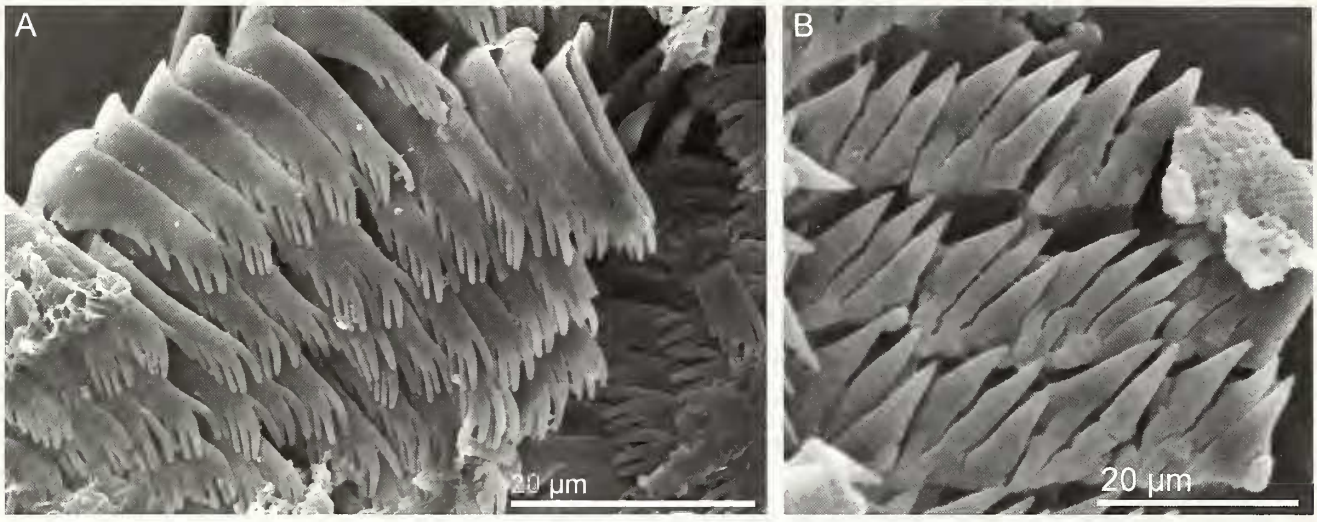

Figure 4. Scanning electron micrographs of a paratype of *F. sisalensis* (CNMO 2981). A. Outer teeth. B. Jaw rodlets.

with all denticles similar in size (non bicuspid) and short jaw rodlets with more than two cusps. These species are *Felimare kempfi*, *F. molloi*, *F. garciagomezi*, and *F. francoisae*. Additionally, molecular data confirms a closer relationship between these species versus species of *Felimare* with bicuspid teeth. Thus, the new species *F. sisalensis*, which has a similar radular and jaw morphology, is compared only to Atlantic species of *Felimare* with non-bicuspid teeth.

All *Felimare* species previously assigned to *Mexichromis* are very uncommon, with no more than eight specimens found per survey even in the case of *F. kempfi* (Meyer, 1977), which is the most common species. Most of these *Felimare* species have restricted geographic ranges. *Felimare francoisae* has been reported only for Cape Verde and Senegal (Bouchet and Ortea, 1980; Ortea et al., 1996). The material from Ghana assigned to *Hypselodoris tricolor* by Edmunds (1981) was described as the new species *M. garciagomezi* by Ortea et al. (1996), because of its distinct external coloration, radula and jaw morphology. This species has not been collected ever since Edmunds's (1981) record. *Felimare molloi*

Table 1. Character comparison of Atlantic species of *Felimare* traditionally assigned to *Mexichromis*.

Species	Mantle Glands	Jaw rodlets (number)	Radular formula	Branchial leaves	Geographic range	References
F. francoisae	On anterior and posterior ends of body	3–4	45×30.0.30	12	Senegal and Cape Verde	Bouchet & Ortea, 1980; Ortea, 1988; Ortea et al., 1996
F. garciagomezi	On each side of rhinophores and on the posterior end of body	3–4	23×12.0.12	6 (8 mm specimen) 4 (3.5 mm specimen)	Ghana	Edmunds, 1981
F. kempfi	not observed	3–5	50×35.0.35	9	USA (Florida), Mexico (Quintana Roo), Panama, Costa Rica, Colombia, Brazil, Puerto Rico	Marcus, 1970; Meyer, 1977; Collin et al., 2005; Valdés et al., 2006; Ardila, et al., 2007; Ortigosa Gutiérrez, 2009
F. molloi	On each side of rhinophores and on the posterior end of body	4	28×17.0.17	10	Isla Picuda (Venezuela)	Ortea et al., 1996
F. sisalensis	All around except for anterior end	3–4	32×20.0.20	9	Mexico (Yucatán)	Present study

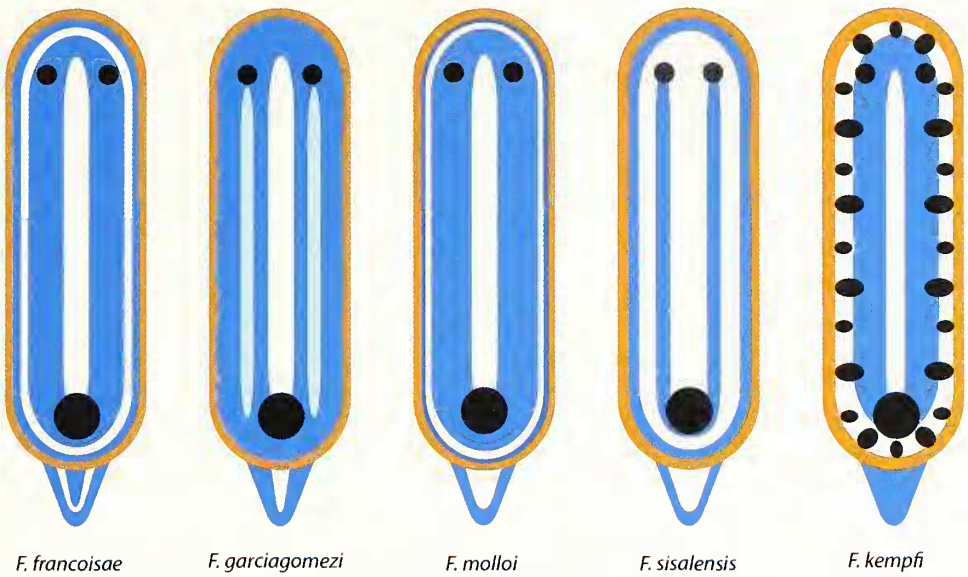

Figure 5. Schematic representation of the color pattern of the Atlantic species of *Felimare* previously assigned to *Mexichromis*.

was originally described based on a single specimen collected in Isla Picuda, Venezuela (Ortea et al., 1996) and never cited again. *Felimare kempfi* is the only species with a relatively broad geographic range including Florida, Mexico, Panama, Costa Rica, Puerto Rico, and Brazil and also in two reefs of the Campeche bank (Table 1). All these species seem to live in shallow waters; the deepest record is for *F. kempfi* in Brazil, at 37 m depth (Marcus, 1971).

Felimare sisalensis can be distinguished easily from those other four species by its external coloration (Figure 5). *Felimare kempfi* is a primarily blue species with a longitudinal white band that runs from between the rhinophores to the gill and a series of elongate black spots on each side of this band, whereas in *F. sisalensis* is mainly white with two blue lines that run from each rhinophore to the gill. Ortigosa-Gutiérrez (2009) reported specimens of *F. kempfi* collected from another reef of the Campeche Bank and similar in size to the type material of *F. sisalensis* (7 and 12 mm long), and the black spots are visible (Figure 2C–D). Valdés et al. (2006) suggested the possibility that *F. molloi* could be a synonym of *F. kempfi*, which would lack black spots as juveniles, but Ortigosa-Gutiérrez's (2009) record suggests that *F. molloi* is indeed a distinct species. *Felimare molloi* has also a white band that runs from between the rhinophores to the gill and instead of the black spots of *F. kempfi*, it has a blue band surrounded by irregular areas of white color. *Felimare garciagomezi* is almost completely blue, with a central white line that runs from the middle of the rhinophores to the gill and two shorter pale blue lines on each side of the central line that do not surround the rhinophores.

The radular and jaw morphology of *F. kempfi* and *F. sisalensis* are very similar, both species lack rachidian teeth, and the outer radular teeth have 6 cusps; the jaw rodlets have 3–4 cusps in both species (Table 1). The radula of the eastern Atlantic species *F. francoisae* is different from that of *F. sisalensis* as it has more cusps on the outer radular teeth (10–11) and the jaw rodlets have 3–6 cusps instead of 3-4 in *F. sisalensis*. Finally *F. garciagomezi* has finely denticulate outer radular teeth (Edmunds, 1981) and jaw rodlets with 3–4 cusps (Table 1).

The only two species for which the reproductive system has been described and illustrated are *F. francoisae* (in Bouchet and Ortea, 1980; Ortea et al., 1996) and *F. molloi* (in Ortea et al., 1996). The reproductive system of *F. sisalensis* is clearly distinguishable from that of *F. francoisae* and *F. molloi* because the seminal receptacle is not connected directly into the bursa copulatrix as in these two species. Additionally, in *F. sisalensis* the deferent duct is wider than that of *F. francoisae*. A vestibular gland was not observed in *F. sisalensis*, but it was reported in *F. francoisae* and *F. molloi* by Ortea et al. (1996).

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LITERATURE CITED

Aikake, H. 1974. A new look at the statistical model identifications. IEEE Trans Auto Control 19: 716–723.

Ardila, N.E., D.P. Báez, and A. Valdés. 2007. Babosas y liebres de Mar (Mollusca: Gastropoda: Opisthobranchia) de Colombia. Biota Colombiana 8: 185–197.

Bertsch, H. 1977. The Chromodoridinae nudibranchs form the Pacific Coast of America. Part I. Investigative methods and supra-specific taxonomy. The Veliger 20: 107–118.

Bouchet, P. and J. Ortea. 1980. Quelques Chromodorididae bleus (Mollusca,Gastropoda, Nudibranchiata) de l'Atlantique Oriental. Annales de l'Institut Océanographique 56: 117–125.

Collin, R., M.C. Diaz, J. Norenburg, R.M. Rocha, J.A. Sanchez, A. Schulze, M. Schwartz, and A. Valdés. 2005. Photographic Identification Guide to Some Common Marine Invertebrates of Bocas Del Toro, Panama. Caribbean Journal of Science 41: 638–707.

Edmunds, M. 1981. Opisthobranchiate Mollusca from Ghana: Chromodorididae. Zoological Journal of the Linnean Society 72: 175–201.

Huelsenbeck, J.P. and F. Ronquist. 2001. MrBayes: Bayesian inference of phylogeny. Bioinformatics 17:754–755. doi:10.1093/bioinformatics/17.8.754

Johnson, R. and T.M. Gosliner. 2012. Traditional taxonomic groupings mask evolutionary history: A molecular phylogeny and new classification of the chromodorid nudibranchs. PLoS ONE 7(4): e33479. doi:10.1371/journal.pone.0033479.

Marcus, Ev. 1971. Opisthobranchs from northern Brazil. Bulletin of Marine Science 20: 922–995.

Meyer, K.B. 1977. Dorid Nudibranchs of the Caribbean coast of the Panama Canal Zone. Bulletin of Marine Science 27: 299–307.

Nylander, J.A.A. 2004. MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Ornelas-Gatdula, E., A. DuPont, and Á. Valdés. 2011. The tail tells the tale: taxonomy and biogeography of some Atlantic *Chelidonura* (Gastropoda: Cephalaspidea: Aglajidae) inferred from nuclear and mitochondrial gene data. Zoological Journal of the Linnean Society 163: 1077–1095.

Ortea, J. 1988. Moluscos opistobranquios del Archipiélago de Cabo Verde: Chromodorididae. Publicações Ocassionais da Sociedade Portuguesa de Malacologia 11: 1–16.

Ortea, J., Á. Valdés, and J.C. García-Gómez. 1996. Revisión de las especies Atlánticas de la familia Chromodorididae (Mollusca: Nudibranchia) del grupo cromático azul. Avicennia supplement 1:1–165.

Ortigosa-Gutiérrez, J.D. 2009. Biogeografía de moluscos opistobranquios de Yucatán, México. Master Thesis. Universidad Nacional Autónoma de México, 97 pp.

Palumbi, S.R. 1996. Nucleic acids II: the polymerase chain reaction. In: Hillis DM, Moritz C, Mable BK, eds. Molecular systematics. Sunderland, MA: Sinauer Associates, 205–247.

Rudman, W.B. 1983. The Chromodorididae (Opisthobranchia, Mollusca) of the Indo-West Pacific: *Chromodoris splendida*, *C. aspersa* and *Hypselodoris placida* colour groups. Zoological Journal of the Linnean Society 78: 105–173.

Rudman, W.B. 1984. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. Zoological Journal of the Linnean Society 81: 115–273.

Spalding, M.D. 2004. A guide to the coral reefs of the Caribbean. University of California Press, Berkeley, 256 pp.

Valdés, A., J. Hamann, D.W. Behrens and A. DuPont. 2006. Caribbean Sea Slugs: A Field Guide to the Opisthobranch Mollusks from the Tropical Northwestern Atlantic. Sea Challengers Natural Hystory Books, Gig Harbor, 289 pp.

Zarco-Perelló, S. 2008. Descripción fisiográfica de los arrecifes de Sisal y hábitats del arrecife Madagascar, Yucatán, México. Undergraduate Thesis. Universidad Nacional Autónoma de México, 104 pp.